REVIEW

Recent history, current status, conservation and management of native mammalian carnivore species in Great Britain

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ABSTRACT

1. After historical declines in population sizes and ranges, we compare and contrast the recent history and contemporary variation in the status of Great Britain's eight native mammalian carnivore species from the 1960s to 2017.
2. Wildcat *Felis silvestris* conservation status is unfavourable and is masked by hybridisation with domestic cats *Felis catus*. Red foxes *Vulpes vulpes* remain widespread but are currently declining. European otter *Lutra lutra*, European pine marten *Martes martes* and European polecat *Mustela putorius* populations are characterised by rapid recovery. Otters have almost completely recolonised Great Britain, polecats have expanded their range throughout southern Britain from refugia in Wales and pine martens have expanded their range from the Scottish Highlands. European badgers *Meles meles* have generally increased in population density. Status assessments of stoats *Mustela erminea* and weasels *Mustela nivalis* are data-deficient but available evidence suggests that stoats may have increased while weasels may have declined.
3. Anthropogenic processes influencing carnivore status include legal protections, habitat quality, reintroductions, predator control, pollutants, hybridisation and diseases and associated control practices. Population effects of pollutants, such as anticoagulant rodenticides, remain poorly characterised. The widespread interface with domestic and feral cats makes the wildcat's situation precarious. Recent declines in rabbit *Oryctolagus cuniculus* populations are a concern, given that several carnivore species depend on them as food.
4. We conclude that, with the exception of the wildcat, the status of Great Britain's mammalian carnivores has markedly improved since the 1960s. Better

understanding of the social aspects of interactions between humans and expanding predator populations is needed if conflict is to be avoided and long-term co-existence with people is to be possible.

Keywords: carnivores, hybridisation, monitoring, pollutants, predator control

Running head: Carnivores in Great Britain

INTRODUCTION

Eight species of terrestrial mammalian carnivore are native to, and extant in, Great Britain (defined here as England, Scotland, Wales and their islands): wildcat *Felis silvestris*, red fox *Vulpes vulpes*, European otter *Lutra lutra*, European badger *Meles meles*, European pine marten *Martes martes*, stoat *Mustela erminea*, weasel *Mustela nivalis* and European polecat *Mustela putorius*. Since their arrival 5000–20000 years ago (Montgomery et al. 2014), they have had mixed fortunes, depending in part on whether they were reviled as vermin, used for sport, valued for fur, appreciated as rodent-catchers, or combinations thereof during their shared histories with humans (Lovegrove 2007). Langley and Yalden (1977) illustrated the eighteenth and nineteenth century declines of what they termed Britain's 'rarer carnivores' (wildcat, pine marten and polecat), which they attributed largely to intensive predator control by gamekeepers, leading to persistence only in refugia where control was least intensive. Otter and badger populations were also greatly reduced but did not experience such pronounced range contractions (Cresswell et al. 1989, Jefferies 1989), despite local pressures from digging (Cresswell et al. 1989) or hunting (Jefferies 1989). By the twentieth century, only fox, stoat and weasel appeared unaffected by control (Tapper 1992). The advent of World War I, cessation of sporting activities and the loss of a generation of gamekeepers led to a reduction in predator control (Langley & Yalden 1977). Contemporaneous reports suggest that the most affected species showed signs of recovery almost immediately (Lovegrove 2007). By the 1970s, there was evidence that the wildcat, pine marten and polecat were beginning to recolonise their former ranges (Langley & Yalden 1977). Otters, however, were experiencing catastrophic decline

(Jefferies 1989), later ascribed primarily to exposure to organochlorine pesticides (Chanin & Jefferies 1978).

Since the 1970s, legal, social and practical developments have altered the anthropogenic pressures faced by Britain's carnivores. Management practices have changed, with bans on certain traps and toxicants, and greater reliance on rearing and releasing pheasants *Phasianus colchicus*, as opposed to fostering wild gamebirds (Tapper 1992). Legal protections have been put in place internationally (e.g. the European Union's Habitats Directive 1992) and nationally for conservation (e.g. Wildlife & Countryside Act 1981) and on animal welfare grounds (e.g. Protection of Badgers Act 1992). Land use change (Swetnam 2007) and agricultural intensification have been associated with biodiversity loss (Robinson & Sutherland 2002). The mechanisms and implications of exposure to some contaminants are now better understood (Shore & Rattner 2001), advances in genetics have revealed the extent of hybridisation between wild and domestic species (Driscoll et al. 2007, Costa et al. 2013), and developments in epidemiology have enhanced knowledge of carnivores as disease reservoirs (Delahay et al. 2009).

A century after the rarest of Britain's carnivores reached their nadir and forty years after the publication of the paper by Langley and Yalden (1977), it is timely to compare and contrast the status of the eight species. We have gathered literature from the 1960s to 2018 and include the latest population estimates. We review processes that affect carnivores, positively and negatively. Although two non-native carnivore species, feral ferret *Mustela furo* and American mink *Neovison vison*, have become established in Great Britain, they are not considered here, other than as an influence on native species.

METHODS

We searched Scopus, Google Scholar and Google using scientific and common names (wildcat, [red] fox, [European] otter, [European] badger, [European] pine marten, stoat, weasel, [European] polecat) and the keywords 'Britain', 'England', 'Scotland' or 'Wales' and 'distribution', 'density' and 'monitoring'. Publications until 5 October 2018 comprising systematic surveys of distribution and abundance were catalogued. Further publications were added from their citations. *Ad hoc* records were not included because of the difficulty of distinguishing hybrids (wildcats and polecats) and because our objective was to assess status using large-scale accounts.

Distribution data were digitised (QGIS Development Team 2009) and scaled to hectads. Range expansion, if any, was modelled following Preuss et al. (2014). Only surveys using comparable approaches, i.e. nationwide surveys using carcass collection and verifiable sightings, were included. Central points of the 1960-1975 core ranges (Langley & Yalden 1977) were used as the starting point from which later expansion was measured. For wildcats the starting point was Scotland, for pine martens it was northern Scotland, and polecats it was central Wales. Range change was measured between starting points and range margins in each decade. Distances from central points were measured to the centre of each hectad in which presence was confirmed in later surveys. Outliers unlikely to be part of a contiguous population were removed. Range margins were estimated by fitting a gamma distribution to distance to central point data, using the 95^{th} quantile to represent the location of the range edge. This approach was preferred as it is less sensitive to sampling variation (Preuss et al. 2014). The slope of the regression with time was taken as the rate of expansion.

POPULATION CHANGE AND CURRENT STATUS

Wildcat *Felis silvestris*

The wildcat's range diminished earlier than those of pine marten or polecat. In 1915 wildcats were limited to the Scottish Highlands, showing the most restricted distribution of Langley and Yalden's (1977) rarer carnivores. By the 1970s, wildcats could be loosely grouped into two populations: a south-western population in the southern Highlands, Argyll and Bute; and a north to north-eastern population stretching from the north-central Highlands to the Grampians (Langley & Yalden 1977). Three distribution surveys using carcass collection, live trapping and sightings were undertaken between the 1980s and 2010s (Fig. 1). An intensive camera-trapping survey was also carried out by Kilshaw et al. (2016) to assess wildcat occupancy with habitat covariates. It is difficult to assess changes in wildcat distribution, or to model range expansion, owing to the presence of, and changes in reporting of, hybrids (Fig. 1). Our model of wildcat range change was inconclusive (expansion rate 0.2 km per year over 30 years, 95% confidence interval: -4.4 to 4.9, Appendix S1b). In the 1980s, wildcats were distributed throughout northern and central Scotland and there was an increase in records in the east of the country and an expansion of range north-east into Caithness, compared to the 1970s (Easterbee et al. 1991). The two population groupings (Langley & Yalden 1977) were less evident. Davis and Gray (2010) divided records into 'possible' (44%) and 'probable' (56%) wildcat sightings, using pelage characteristics (Kitchener et al. 2005). 'Probable' wildcat records were more common north of the Highland boundary line than 'possible' wildcat records, which appeared more frequently in the south and east of Scotland. Wildcat distribution is currently assumed to be that of the 'probable' records (Scottish Natural Heritage 2013). Kilshaw et al. (2016) reported that the probability of wildcat occupancy is highest in the central and eastern Highlands, the edges of the Cairngorms, along the west coast and in a few areas in the far north. The Scottish Wildcat Action project has not received any records verified as wildcats from the northern Highlands since 2015 (R. Campbell, unpublished data). It is also believed that there are no wildcats south of central Scotland (Kilshaw et al. 2016). The latest population estimate for wildcats is 200 (95% confidence interval: 30 – 430; Mathews et al. 2018; Appendix S2). However, the reliability of this estimate is considered to be low and estimates vary depending on how strict a definition of wildcat is used.

Red fox *Vulpes vulpes*

Red foxes are present throughout mainland Great Britain, Anglesey, Isle of Wight and Skye (Harris et al. 1995, Webbon et al. 2004). It is likely that the species' value in sport hunting meant that foxes were protected to some degree from systematic control and this prevented the historic declines seen in other carnivores (Tapper 1992). Foxes feature in numerous surveys, including the Game and Wildlife Conservation Trust's (GWCT) National Gamebag Census (NGC; Aebischer et al. 2011) and the British Trust for Ornithology's (BTO) Breeding Birds Survey (BBS). The NGC provides a long-term index of individuals killed per unit area as part of game management and NGC records of foxes killed on game estates suggest a population increase in Britain from the 1960s, followed by stabilisation from the 1990s to 2009 (Fig. 2; Aebischer et al. 2011). Data from the BBS over a similar time period partly corroborate this; however, recent data indicate a 45% decline in the numbers of foxes seen on BBS sites in England (-41% throughout the United Kingdom) from 1996-2016, particularly after *c.* 2008 (BTO 2018, Harris et al. 2018). There are no other data to corroborate this decline and causes are not understood, though timing is coincident with significant declines in BBS records of rabbits *Oryctolagus cuniculus* in England (-44%), Scotland (-82%) and Wales (-48%; Harris et al. 2018).

Previous causes of fox declines include hunting pressure (Tapper 1992) and localised outbreaks of mange caused by *Sarcoptes scabiei* (Soulsbury et al. 2007). Some of these declines have been offset by spread into areas or habitats where foxes were previously scarce (Baker et al. 2006), such as Norfolk (Tapper 1992) and urban spaces (Scott et al. 2014). A survey of England and Wales found that in the 2010s foxes were recorded in ~90% of 65 cities, where they had been scarce or absent in the 1980s (Scott et al. 2014). Although urban foxes are increasing, they still comprise a small proportion of the total population. Webbon et al. (2004) estimated the total rural fox population in Britain to be 225000, whereas the estimate for urban foxes was 33000 in 1995 (Harris et al. 1995). The latest estimate of the total fox population is 357000 (95% confidence interval: 104000 - 646000; Mathews et al. 2018; Appendix S2).

European otter *Lutra lutra*

As an apparent competitor with humans for fish, the European otter has long been viewed as a pest. Otter hunting began in the Middle Ages (Lovegrove 2007). Historical records indicated a slow decline in numbers from the late eighteenth century onwards, caused by predator control, sport hunting with hounds and pollution (Jefferies 1989). Otters rarely scavenge and have large territories, making them less likely than other carnivores to enter baited traps (Jefferies 1989). While local extinctions occurred in some catchments, regional extinctions were initially avoided (Harris et al. 1995).

By the late 1950s, hunt records indicated that otters were experiencing sudden and rapid decline, with the most severe reductions in southern England (Jefferies 1989).

Various potential drivers were considered, including habitat destruction, disturbance, introduction of American mink, the associated spread of canine distemper virus, hunting pressure and the possibility of increased mortality arising from the severe winter weather of 1962-3 (Chanin & Jefferies 1978). The timing and sudden onset of the decline, simultaneous to that observed in predatory birds, suggested that organochlorine pesticides, principally dieldrin, were likely to be responsible for increased mortality (Chanin & Jefferies 1978). Dieldrin, introduced in the 1950s as a sheep dip and seed dressing, was detected in 81% of otters examined between 1963 and 1973 (Mason et al. 1986). Voluntary restrictions were placed on dieldrin use in the 1960s and 1970s, followed by mandatory bans in the 1980s (Macdonald 1983).

National otter surveys began in the 1970s (Fig. 3, Appendix S3), when otters were recorded at only 6% of sites in England (Lenton et al. 1980), 20% in Wales (Crawford et al. 1979) and 57% in Scotland (Green & Green 1980). By the 1980s, European otters were present at 10% of sites in England (Strachan et al. 1990), 38% in Wales (Andrews & Crawford 1986) and 65% in Scotland (Green & Green 1987). Reintroductions were carried out in East Anglia, Hertfordshire and the upper Thames in the 1980s and early 1990s (Jefferies et al. 1986, Harris et al. 1995, Roche et al. 1995). Surveys in the 1990s recorded otters present at 23% of sites in England (Strachan & Jefferies 1996), 53% in Wales (Andrews et al. 1993) and 88% in Scotland (Green & Green 1997). By the 2000s, European otters were recorded at 36% of sites in England (Crawford 2003), 72% in Wales (Jones & Jones 2004) and 92% in Scotland (Strachan 2007). The most recent surveys found European otters at 59% of the original sites surveyed in England (Crawford 2010) and, when accompanied by spot checks in areas not covered by the original surveys, these data show that only Kent and East Sussex are yet to be substantially recolonised (Fig. 3). Otters are considered to be at carrying capacity in south-west England and the Wye Valley, with evidence of otter presence at over 80% of sites (Crawford 2010). The 2009-10 survey in Wales indicated otter presence at 90% of sites (Strachan 2015). The contemporaneous survey in Scotland indicated that there may have been a decline in occupancy since the previous decade, with detection at 78-80% of sites surveyed (Findlay et al. 2015). However, there was some uncertainty as to whether this was a real decline or a result of inclement weather during surveying and reduced detectability (Findlay et al. 2015). Otters are now widespread throughout both Wales and Scotland (Fig. 3). In England, Crawford (2010) estimated that otter distribution had expanded at approximately 3.6 km per year, and this trend is expected to lead to complete recolonisation of England, and therefore Great Britain, by 2030 (Crawford 2010).

Dieldrin is still detectable in otters (Chadwick 2007) but is not considered likely to affect populations at the observed trace levels (Crawford 2010). The presence of invasive American mink, which became widespread during the otters' absence, has not impeded otter recolonisation, probably because otters cause shifts in mink behaviour (Harrington et al. 2009). The latest population estimate for otters in Britain is 11000, although the reliability of this estimate is considered to be very low (Mathews et al. 2018; Appendix S2).

European badger *Meles meles*

European badger populations declined during the nineteenth century to the extent that the species were considered uncommon (Cresswell et al. 1989). Declines were due to a combination of control by gamekeepers, sett disturbance and badger baiting (Wilson et al. 1997). The extent of pressure varied regionally. For example, in East Anglia, intensive activity by gamekeepers reduced numbers to a tenth of those in neighbouring counties (Harris 1993).

By the 1970s, badgers were more common in south-west and central England, and central and north Wales (Appendix S3), but remained unrecorded in parts of East Anglia and northern Scotland (Neal 1972). In the 1980s, badger distribution expanded and the population was estimated to be 250000 in Great Britain, although gaps remained in London, East Anglia, Lincolnshire, Lancashire and northern Scotland (Cresswell et al. 1990). By 1994-97, the number of badger social groups in Britain had increased by 24%, although colonisation of new areas was minimal (Wilson et al. 1997).

In 2006-09, surveys of mainland Scotland indicated that badger main sett numbers had increased since the 1990s, though differences in methodology made direct comparisons difficult (Rainey et al. 2009). In England and Wales, numbers of badger social groups increased by 88% (equivalent to 2.6% per annum) between 1985-88 and 2011-13 (Judge et al. 2014). The magnitude of changes in sett density varied by region, due to a combination of landscape and local effects. England saw a 103% increase, whereas in Wales densities remained stable (Judge et al. 2014). Combining results from Scotland (Rainey et al. 2009), with Judge et al. (2014), leads to an estimate of 81000 (95% confidence interval: 75400–86600) badger social groups in Britain by 2013. Judge et al. (2017) combined their earlier sett survey with analysis of social group size variation, to derive a population estimate of 485000 individual badgers in England and Wales. Even allowing for methodological differences, evidence suggests that badger populations increased substantially in England and Wales between the 1980s and 2011-13 (Cresswell et al. 1990, Judge et al. 2017).

European pine marten *Martes martes*

When the European pine marten population reached its nadir in *c*. 1915, its range was restricted to the north-west of the Scottish Highlands and small, isolated areas of northern England and north Wales (Langley & Yalden 1977). By 1975, there was some spread eastwards into the Scottish Grampians, while the Welsh population was not thought to have expanded and English records were limited to sporadic sightings in Yorkshire and the Lake District (Langley & Yalden 1977).

By the 1980s in Scotland, the main populations were still confined to north of the Great Glen, though pine marten occurrence was nearly continuous throughout the central and western Highlands (Velander 1983). As the prevailing view was that this northern population was too remote to recolonise southern Scotland, a reintroduction took place in Galloway Forest, southwest Scotland in 1980 and 1981 (Shaw & Livingstone 1992). In the 1990s, pine martens expanded south of the Highlands into Argyll and Bute, Stirling and Perth and Kinross. By 2013, they had been recorded throughout much of central and eastern Scotland, on Skye and Mull and beyond the release sites in Galloway (Fig. 4; Croose et al. 2013, 2014). Our model of range expansion estimates that between 1975 and 2015 the Scottish pine marten population expanded at a rate of 1.7 km per year (95% confidence interval: 0.8-2.7 km, Appendix S1b). Despite repeated surveys during the 1980s and 1990s (Appendix S3), evidence of pine marten presence in England and Wales remained limited, suggesting that at best only a few low-density populations remained. There is occasional evidence of pine martens from Shropshire and Hampshire, potentially the result of covert releases. Recent evidence in Northumberland indicates that European pine martens are expanding south through the Borders, recolonising parts of northern England (Vincent Wildlife Trust [VWT], unpublished data). Between 2015 and 2017, 51 pine martens were translocated from Scotland to Wales in order to reinforce populations there; this has proven successful with high survival and breeding in the wild (VWT, unpublished data). The latest population estimate for pine martens is 3700 (95% confidence interval: 1600 - 8900; Mathews et al. 2018; Appendix S2).

Stoat (ermine) ***Mustela erminea***

There are no national surveys for the stoat and so data are from the GWCT's NGC. Stoats are thought to be common and widespread throughout Great Britain, including on the Isle of Wight and the Scottish islands of Shetland, Islay, Jura, Mull, Skye, Raasay and Bute (McDonald & King 2008a). In 2010 stoats were sighted for the first time on Mainland, Orkney and an eradication programme is underway there in an attempt to protect ground-nesting birds, Orkney voles *Microtus arvalis orcadensis* and the predatory birds that eat them (Fraser et al. 2015). In spite of intensive predator control in the nineteenth century, stoat numbers did not exhibit the declines seen amongst the larger mustelids (Tapper 1992). This is likely to be due to the stoat's high productivity, reducing potential for culling to cause decline, and its mobility, facilitating immigration into areas where numbers are reduced (McDonald & Harris 2002).

Stoat numbers were severely reduced by myxomatosis in rabbits (Sumption & Flowerdew 1985). One game estate in Suffolk reported a tenfold reduction in the numbers of stoats killed in the years after the initial outbreak (Tapper 1992). Stoats were, and remain, extremely reliant on rabbits (McDonald et al. 2000) and the loss of this important food source was believed to have impaired productivity and survival (Sumption & Flowerdew 1985). The NGC shows that indices of the numbers of stoats killed per unit area on game estates increased steadily from the 1960s (Fig. 5; Aebischer et al. 2011), alongside rabbit recovery, though the NGC reported another dip in stoats killed in the 1980s (Aebischer et al. 2011). In a comparative study of stoat and weasel diets between the 1960s and 1990s, McDonald et al. (2000) concluded that there was little evidence that reductions in prey were causing this downturn, some of which may have been attributable instead to changes in trapping effort affecting the NGC (McDonald & Harris 1999). Since then, there has been a steady increase in stoats killed on game estates from the 1990s to 2009 (Fig. 5). The impact on stoats of the recent apparent reductions in rabbit numbers is unknown. The latest population estimate for stoats is 438000 (Mathews et al. 2018), unchanged from that of Harris et al. (1995), indicating the sparsity of data. Both of these estimates are considered to have low reliability (Appendix S2).

Weasel (common weasel, least weasel) *Mustela nivalis*

Weasel population trends are also from the GWCT's NGC. Weasels are relatively prolific breeders and, similar to stoats, did not appear to experience nineteenth century declines (Tapper 1992). They are also thought to be common and widespread throughout mainland Great Britain (McDonald & King 2008b). In contrast to stoats, weasel abundance increased during and after myxomatosis, likely a result of reduced rabbit grazing, increased rough grassland and increased abundance of field voles *Microtus agrestis* (Jefferies & Pendlebury 1968), which are frequent prey of weasels (McDonald et al. 2000).

The NGC reveals a decline in indices of weasels killed per unit area on game estates from the 1960s onwards (Fig. 5). Models of weasel populations suggest that this decline is unlikely to be the result of trapping by gamekeepers as, similar to stoat, the weasel's high productivity and mobility buffer populations against intense culling (McDonald &

Harris 2002). Weasel productivity is particularly sensitive to prey abundance (King 1980) and populations fluctuate with vole abundance (Tapper 1979). It is therefore possible that there has been a negative effect of rabbit recovery on field vole populations and, consequently, weasels (Sumption & Flowerdew 1985). Weasel indices from the NGC started to increase again from the 1990s but are still below those recorded in the 1960s (Fig. 5). The latest population estimate for weasels is 450000 (Mathews et al. 2018). In common with stoats, this estimate is the same as that of Harris et al (1995), indicating the paucity of data for these species (Appendix S2).

European polecat *Mustela putorius*

Having reached their nadir in *c.* 1915, European polecat populations began to recover following the alleviation of predator control during the early twentieth century, the banning of gin traps in 1958, and the recovery of rabbit populations after the myxomatosis epizootic of the mid-twentieth century (Langley & Yalden 1977). Rabbits are also important prey for polecats (Birks & Kitchener 1999) and, although rabbits were previously abundant, they were catastrophically reduced as the disease swept across the country (Sumption & Flowerdew 1985). Rabbit numbers began to recover by the 1960s and by the 2000s were approaching pre-myxomatosis levels (Aebischer et al. 2011), although more recently rabbits have experienced significant declines (see the Red Fox section). Reports suggest that polecats were already expanding their range by the 1960s but rabbit and polecat recovery are likely to be closely linked (Sumption & Flowerdew 1985).

National polecat surveys have taken place between the 1980s and 2010s (Appendix S3). From the 1990s, surveys attempted to distinguish between polecats and hybrid polecat-ferrets, based on a pelage classification system (Birks & Kitchener 1999). Classifications of carcasses in this way and, more recently, using molecular genetic techniques, suggest that polecat-ferrets are more prevalent at the edge of the polecat's range (Costa et al. 2013).

In the 1980s, polecats occupied most of Wales and the border counties of Shropshire and Worcestershire (Tapper 1992). By the 1990s, polecats were present in all counties on the English side of the Welsh border (Birks & Kitchener 1999). The 2000s were characterised by increased density of records in Derbyshire, Buckinghamshire, Berkshire, Wiltshire, Dorset and Hampshire (Birks 2008). Unofficial releases led to polecats becoming established in Cumbria, Argyll and Perthshire, well outside of the core range, though the pelage characteristics of some of these animals suggested they were from captive stock (Birks 2008). By 2015, polecats had recolonised most of central and southern England (Fig. 6) and remained widespread in Wales and the West Midlands (Croose 2016). The most noticeable gaps in current distribution are in northern England and Scotland, potentially due to difficulties in dispersing around conurbations. Overall, the polecat's range expanded eastwards at 4.9 km per year between 1975 and 2015 (95% confidence interval: 2.6-7.1 km, Fig. 6, Appendix S1b). This is faster than the pine marten's expansion, which is not unexpected; polecats have faster reproductive ability and greater flexibility in habitat requirements than pine martens (Birks 2015, 2017). The latest population estimate for polecats is 83300 (95% confidence interval: 68000 - 99000; Mathews et al. 2018; Appendix S2).

ANTHROPOGENIC PROCESSES AFFECTING CARNIVORE STATUS

Legislation

There are various legal protections for carnivores in Great Britain (Fig. 7, Appendix S4). Protections that ban direct control and disturbance are likely to aid species recovery where these pressures were a cause of population decline. Range expansions and population increases have occurred for some species (notably otters, badgers, pine martens and polecats) following the introduction of legal protection. However, legal protection is less effective where non-compliance is high, or where other factors beyond the legal mandate are limiting populations. Hybrid animals create a particular legal difficulty, as hybrids are not usually protected, even when sympatric 'pure' wild types are (Trouwborst 2014). 'Pure' animals may be confused with hybrids by hunters, leading to inadvertent killing. While badger recovery in Great Britain has been coincident with legislation, badger populations elsewhere have not increased following legal protection. For example, badger populations in Northern Ireland appear to be constrained by climate, habitat, farming practices or food availability, rather than by persecution (Reid et al. 2012).

Habitat quantity, quality and connectivity

Habitat loss and fragmentation are major contributing factors to biodiversity loss and can be more significant for habitat specialists (otters and pine martens) than for generalists that are better able to exploit modified landscapes (foxes, stoats and weasels; Bright 1993, Crawford 2010). Habitat fragmentation may increase intra-guild predation among carnivores, as has been observed between foxes and pine martens (Lindström et al. 1995). To counter habitat loss, a series of international and national regulations aimed at protecting habitat extent and quality have been implemented over the last six decades, including the European Union's Habitats Directive and Water Framework Directive. The result has been a wide-ranging protected area network that includes Special Areas of Conservation, Ramsar wetlands, national parks, and Sites or Areas of Special Scientific Interest. Existing habitats have been enriched via the creation and maintenance of den sites for otters and pine martens (Chanin 2003, Croose et al. 2016) and the promotion of wildcat-friendly forestry management in wildcat priority areas (Scottish Natural Heritage 2013). More generally, afforestation since the 1950s, notably in Scotland, has provided additional, if not ideal, habitat for pine martens (e.g. Croose et al. 2013, 2014). Even with the protected area network, a lack of connectivity, through fragmentation or via natural or anthropogenic barriers, may prevent dispersal. Many monitoring tools rely on collecting road casualty carcasses, testament that these species are vulnerable to road mortality (Appendix S3). Roads, urban areas and large continuous tracts of other unfavourable habitat may act as physical barriers to recolonisation. Genetic studies on badgers and wildcats suggest that while large roads can have a significant impact on gene flow, they are not impermeable, as animals can utilise crossing points (Frantz et al. 2010, Hartmann et al. 2013). Recolonisation of areas that require crossing of landscape barriers may therefore be possible, but the rate of expansion is likely to depend upon barrier size and landscape configuration.

Agricultural intensification and its consequences for biodiversity are well documented (e.g. Tattersall & Manley 2003). Agri-environment schemes aimed at mitigating the effects of agricultural intensification have been implemented since the 1980s, the most recent being the Environmental Stewardship scheme, which was introduced in 2005. Although Environmental Stewardship has been criticised for its limited benefits and high costs (Kleijn et al. 2011), studies show that it can lead to increases in small mammal abundance (Broughton et al. 2014), potentially benefitting their predators (Johnson & Baker 2003, Askew et al. 2007).

Translocations, releases and escapes

Range expansion and density increase have, in some carnivore species, been assisted by human intervention. Formal conservation translocations have been carried out for otters and pine martens. These may use captive-bred stock, such as for otters (Jefferies et al. 1986) and possible future wildcat releases (Scottish Natural Heritage 2013), or translocations from the wild, such as for pine martens (Shaw & Livingstone 1992, VWT unpublished data). Rehabilitated animals are also released from wildlife rescue centres (Kelly et al. 2010, Mullineaux 2014). Furthermore, unofficial or accidental releases have occurred; examples include polecat releases in Cumbria and Argyll (Birks & Kitchener 1999, Fig. 6) and the arrival of stoats on Orkney (Fraser et al. 2015). Other unofficial releases have been smaller in scale, e.g. there are sporadic records of pine martens in England, where presumably individuals have escaped or been released from fur farms or wildlife collections (Birks & Messenger 2010, Jordan et al. 2012). The extent of, and survival rates of animals from, unofficial releases are unknown, but releases of sufficient scale can sometimes aid expansion. Polecat populations derived from such releases are thriving in Cumbria but apparently dwindling in Argyll (Fig. 6, VWT unpublished data).

Direct control

Nineteenth century declines in carnivore populations are testimony to the impact of intensive control measures, as are the resurgences of some species once control diminished (Langley & Yalden 1977). While managing predators remains central to game management, the intensity of control (with localised exceptions) is unlikely ever to return to pre-1915 levels (Tapper 1992). While some British carnivores are protected from unlicensed predator control, the trapping or shooting of foxes, stoats and weasels is not regulated in practice, other than to prevent cruelty. Land managers applying control must comply with welfare regulations and ensure that control is sufficiently discriminatory to avoid taking legally protected species. Wildcats (Macdonald et al. 2010), otters (Crawford 2010), pine martens (Strachan et al. 1996) and polecats (Packer & Birks 1999) are legally protected from unlicensed control, but are sometimes caught in traps, nets or snares set for other species. The potential for unintentional capture may be greatest in areas that are newly recolonised, as practices that were previously unproblematic may need to be adapted. For species with low reproductive rates, such as pine martens, any additional mortality might impede recovery. The current extent of any intentional or unintentional killing of protected carnivores is unclear. Collaboration between carnivore conservationists and managers of game estates and fisheries is required to find workable solutions for reducing conflicts with expanding carnivore populations. Mitigation methods include electric fencing to prevent carnivores gaining access to pheasant pens (Balharry & Macdonald 1996), exclusion barriers for spring traps (Short & Reynolds 2001) and diversionary feeding and translocations. There is little evidence of the uptake or efficacy of such mitigation methods in practice (Balharry & Macdonald 1996, Thirgood et al. 2000, Graham et al. 2005).

Environmental pollutants

Predators are at particular risk from bioaccumulating and biomagnifying pollutants. Carnivores may be exposed to insecticides, herbicides, fungicides and biocides used for agricultural purposes, a wide range of industrial organic contaminants, toxic metals, and human and veterinary pharmaceuticals (Shore and Rattner 2001, Harrington & Macdonald 2002, Shore et al. 2014). There are relatively few data on current exposure of British carnivores to most of these (Appendix S5).

Although dieldrin is most commonly cited as the cause of otter decline, polychlorinated biphenyls (PCBs) may also have contributed by impairing reproduction in individuals not poisoned by dieldrin (Mason & Wren 2001). The combined effect of dieldrin and PCBs on otters may have been analogous to how dieldrin (acute mortality) and dichlorodiphenyltrichloroethane (DDT; eggshell thinning leading to reproductive failure) caused catastrophic declines in predatory birds (Ratcliffe 1980, Newton 1986). Otters in Britain are also frequently exposed to polybrominated diphenyl ethers (PBDEs; Pountney et al. 2015), which are structurally similar to PCBs and may have a cumulative effect with PCBs (Hallgren & Darnerud 2002), though there is no evidence that exposure of otters in Britain to PCBs and PBDEs is impairing their reproductive output (Pountney et al. 2015).

Second generation anticoagulant rodenticides (SGARs) are widely used to manage rodent populations (Dawson et al. 2003). SGARs disrupt the blood-clotting mechanism (Watt et al. 2005) leading to fatal haemorrhaging. Evidence of sub-lethal effects caused by exposure is uncertain (Van den Brink et al. 2018). Predators are exposed secondarily by consuming contaminated target prey (rats *Rattus norvegicus,* mice *Mus domesticus*) and non-target prey (mice *Apodemus* spp., voles; Tosh et al. 2012, van den Brink et al. 2018). SGAR residues have been detected in most British mammalian carnivores (Appendix S5) and rates of exposure in polecats have increased over the last 20 years (Sainsbury et al. 2018). While mortality caused by rodenticide does occur in mammalian carnivores in Britain (Appendix S5), the extent of this mortality, and whether it affects populations, remains unknown.

Hybridisation

In Britain, hybridisation occurs between wildcats and domestic cats (Driscoll et al. 2007) and between polecats and feral ferrets (Costa et al. 2013). There is also evidence of limited historical hybridisation between European pine martens and American martens *Martes americana* that had presumably escaped from fur farms (Kyle et al. 2003). Hybridisation between wildcats and domestic cats occurs throughout the wildcat's range (Macdonald et al. 2010). Domestic cat DNA is commonly, if not universally, present in Scottish wildcats (Driscoll et al. 2007, Senn & Ogden 2015, Senn et al. 2018), which have experienced the highest levels of introgression among wildcats in Europe (Hertwig et al. 2009). Classifications of wild-living cats using combinations of skull morphology, pelage and genetic techniques suggest that, depending on the definition used, between 40% and 90% of wild-living cats in Scotland do not qualify as 'true' wildcats (Kitchener et al. 2005). Hybrids occupy similar habitat to wildcats, masking potential range expansion, impeding population estimation and perpetuating introgression (Kilshaw et al. 2016). Currently, a 'trap, neuter, vaccinate and return' programme for farm and feral cats is underway in five priority wildcat areas in the Scottish Highlands, with the aim of reducing hybridisation (Scottish Wildcat Action 2018). In comparison to the wildcat, polecat-ferret hybridisation appears less problematic. Analysis by Costa et al. (2013) of polecats collected during the 1990s and 2000s found that 31% of wild polecats were hybrids, with the highest frequency of hybrids at the eastern edges of the polecat's range. First-generation hybrids were not detected, suggesting that the incidence of hybridisation may have been greater in the past (Costa et al. 2013).

Disease and associated interventions

Disease, both naturally occurring and in association with human intervention, can reduce carnivore populations directly. For example, in 1994-1995, sarcoptic mange reduced fox numbers in Bristol by over 95% (Soulsbury et al. 2007). Carnivore populations may also be affected indirectly by disease if it alters the abundance of prey or other sympatric species, as evidenced by changes in stoat and weasel abundance associated with myxomatosis in rabbits (Aebischer et al. 2011). Recent and current effects of rabbit calicivirus on rabbit populations in Britain, and the potential impact on dependent carnivores, is unquantified, although it is possible that rabbit diseases and the associated declines may be contributing to coincident reductions in fox numbers (Harris et al. 2018).

Other indirect consequences may arise from human intervention to control the risk of transmission of zoonoses or diseases of livestock. Wild species may become persistent reservoirs for zoonotic disease (Hassell et al. 2017) and this can lead to control efforts, such as for managing bovine tuberculosis (bTB) in badgers (Wilson et al. 2011). Bovine tuberculosis is enzootic in a large part of the badger population in England and Wales, and badgers are implicated in the spread of the infection to cattle (Delahay et al. 2013). Methods used to control bTB differ between the countries of Great Britain. Scotland, officially free of bTB since September 2009, has no proactive policy for managing the disease in wild animals, the Welsh government has pursued a badger vaccination strategy since 2012 (Welsh Government 2012) and in England proactive, large-scale badger culling is one of a range of policies aimed at eradicating bTB (DEFRA 2011). From 2013 to 2017 inclusive, 34103 badgers were killed as part of licensed culls in England (Giesler & Ares 2018) and 32601 badgers were killed in 2018 (DEFRA & Natural England 2018). Culling aims to reduce badger populations by around 70% in licensed areas and draws on evidence derived from the Randomised Badger Culling Trial (Bourne et al. 2007). This Trial showed that reduced badger numbers resulted in increased fox numbers in cull areas (Trewby et al. 2008), indicating that there may be broader implications for carnivore community structures emerging from badger culling.

CONCLUSIONS

Our aim was to compare and contrast the current status of Britain's mammalian carnivores and the anthropogenic processes that affect their populations. Overall, the outlook for British carnivores is more positive than in the account of decline drawn by Langley and Yalden (1977). Two of their three 'rarer carnivores' (pine marten and polecat) have staged remarkable recoveries, while the third (wildcat) continues to be threatened by hybridisation. Meanwhile, akin to pine martens and polecats, the formerly rare and restricted otter has recovered much of its former range and is increasing in density. Of the nationally distributed species, badgers have increased in population density but are subject to increasingly widespread, intensive culling; foxes have increased but appear to be in a current period of decline; and stoats and weasels remain data-deficient. The recent apparent declines in rabbit records are a cause for concern, given the number of native carnivores that depend on them as food. Since the 1970s there have been significant advances in our understanding of the anthropogenic processes that affect carnivore populations. If humans are to coexist with more abundant carnivores, in more places and in greater diversity, greater emphasis will need to be placed on the social aspects of these processes, whether concerning best-practice use of rodenticides, selective predator control practices, minimisation of hybridisation or management of disease risk.

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Figures

Fig. 1. Wildcat *Felis silvestris* distribution in Scotland from 1960 to 2008. Data are from Langley and Yalden (1977), Easterbee et al. (1991), Daniels et al. (1998), Davis and Gray (2010). Black circles indicate presence. All presence points were scaled to hectads. On the 2000s map, black circles indicate 'probable' wildcats, grey triangles indicate 'possible' wildcats (Davis & Gray 2010). 1992-93 dates are the dates of Daniels et al.'s (1998) live trapping.

Fig. 2. National Gamebag Census index for red fox *Vulpes vulpes* in Great Britain from 1961 to 2009. Gamebags are indices of the numbers killed per unit area on game estates. Index values are relative to the start year, which has an arbitrary value of 1. Error bars represent 95% confidence intervals. Reproduced by permission of the Game and Wildlife Conservation Trust (Aebischer et al. 2011).

Fig. 3. European otter *Lutra lutra* distribution in Great Britain from 1977 to 2012. Maps recreated from National Otter Surveys of England (Lenton et al. 1980, Strachan et al. 1990, Strachan & Jefferies 1996, Crawford 2003, Crawford 2010), Scotland (Green, & Green 1980, Green & Green 1987, Green & Green 1997, Strachan 2007, Findlay et al. 2015) and Wales (Crawford et al. 1979, Andrews & Crawford 1986, Andrews et al. 1993, Jones & Jones 2004, Strachan 2015) using data provided by Environment Agency (2018), Scottish Natural Heritage, Natural Resources Wales and Joint Nature Conservation Committee (2018). Black circles indicate presence. Grey circles indicate surveyed areas where otters were recorded as absent. Blank areas do not indicate absence. 1980s Scotland survey did not include the Western Isles, Northern Isles or the Scottish Highlands (Green & Green 1987). In England, surveys were carried out in alternate 50 x 50 km squares until the most recent survey (Crawford 2010).

Fig. 4. European pine marten *Martes martes* distribution in Great Britain from1960 to 2018. Data from Langley and Yalden (1977), Velander (1983), Bright and Harris (1994), McDonald et al. (1994), Balharry et al. (1996), Strachan et al. (1996), Birks and Messenger (2010), Croose et al. (2013, 2014) and VWT (unpublished data). Black circles indicate presence. All presence points were scaled to hectads. Only verified records in Birks and Messenger (2010) were included. No surveys were carried out in Scotland in the 2000s, and the 2010s Scotland surveys included only central and southern Scotland (Croose 2013, 2014).

Fig. 5. National Gamebag Census indices for stoats *Mustela erminea* and weasels *Mustela nivalis* in Great Britain from1961 to 2009. Black diamonds are for stoats and grey circles are for weasels. Gamebags are indices of the numbers killed per unit area on game estates. All index values are relative to the start year, which has an arbitrary value of 1. Error bars represent 95% confidence intervals. Data reproduced by permission of the Game and Wildlife Conservation Trust (Aebischer et al. 2011).

Fig. 6. European polecat *Mustela putorius* distribution in Great Britain from 1960 to 2016. Data are from Langley and Yalden (1977), Blandford (1987), Tapper (1992), Birks and Kitchener (1999), Birks (2008) and Croose (2016). Black circles indicate presence. Grey triangles indicate polecat-ferret hybrids. All presence points were scaled to hectads.

Fig. 7. Timeline of interventions providing legal protection for native mammalian carnivores in Great Britain.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Changes in the ranges of wildcat *Felis silvestris*, European pine marten *Martes martes* and European polecat *Mustela putorius.* a) Distances (in km) from the central points of species ranges in 1975 to all positive hectads using 95th percentile gamma statistic (after Preuss et al. 2014) and b) results of linear models analysing the rates of expansion (in km).

Appendix S2. Recent population estimates for native mammalian carnivores in Great Britain. Population estimates are the combined totals for England, Scotland and Wales unless otherwise stated. Reliability is scored differently by Mathews et al (2018), where <=1 indicates very poor reliability of estimate and 4 = very good reliability of estimate, and Harris et al (1995), where 1 is most reliable estimate and 5 the least reliable estimate.

Appendix S3. National distribution surveys of native mammalian carnivores in Great Britain, 1960 – 2017.

Appendix S4. National and international legislation providing protection for native mammalian carnivores in Great Britain.

Appendix S5. Incidences of secondary exposure to contaminants in native British mammalian carnivores in Europe.